Russian Entomol. J. 16(4): 385–400

A new taxon Hermanellonota, or subtribe Hermanellini subtr.n. (Ephemeroptera: Leptophlebiidae: Hagenulini), with description of three new species from Peruvian Amazonia

Новый таксон Hermanellonota, или подтриба Hermanellini subtr.n. (Ephemeroptera: Leptophlebiidae: Hagenulini), с описанием трёх новых видов из перуанской Амазонии

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KEY WORDS: Peru, Amazonia, Leptophlebiidae, Hagenulini, Hermanellonota, Hermanellina, *Hermanella*, *Hermanella* (*Hylister*) *chimaera* **sp.n.**, *Simothraulopsis*, *Maculognathus* **subgen.n.**, *Simothraulopsis* (*Maculognathus*) *sabalo* **sp.n.**, *Simothraulopsis* (*Maculognathus*) *plesius* **sp.n.**, *Farrodes*, *Farrodes pakitza*, new subtribe, new subgenus, new species, new combinations, telopenis.

КЛЮЧЕВЫЕ СЛОВА: Перу, Амазония, Leptophlebiidae, Hagenulini, Hermanellonota, Hermanellina, *Hermanella*, *Hermanella* (*Hylister*) *chimaera* **sp.n.**, *Simothraulopsis*, *Maculognathus* **subgen.n.**, *Simothraulopsis* (*Maculognathus*) *sabalo* **sp.n.**, *Simothraulopsis* (*Maculognathus*) *plesius* **sp.n.**, *Farrodes*, новая трибы, новый подрод, новые виды, новые комбинации, телопенис.

ABSTRACT. The taxon Hagenulus/fg1 (or tribe Hagenulini Kluge, 1994) is redefined as including Neotropical taxa Hagenulus/fg2, Hermanella/fg1, Thraulodes/g1, Ulmeritus/g1, Miroculis/g1; it is characterized by complete loss of patella-tibial suture on all legs of larva and adults. A new taxon Hermanellonota **taxon n.**, or Hermanella/fg1 (possible ranking name — subtribe Hermanellina **subtr.n.**) is established; it is characterized by two unique autapomorphies in structure of male genitals and subimaginal mesonotum. Hermanellonota includes *Farrodes*, Simothraulopsis/g1 and Hermanellognatha. Within Simothaulopsis/g1 there is established a new taxon *Maculognathus* **subgen.n.** (which can be regarded as a subgenus of the genus *Simothaulopsis*) with two new species — *Simothraulopsis* (*Maculognathus*) *sabalo* Kluge **sp.n.** and *S.*(*M.*) *plesius* Kluge **sp.n.** Hermanellognatha **taxon n.**, or Hermanella/fg2 (possible ranking name — genus *Hermanella* s.l.) is characterized by unique mouth apparatus and some other larval characters. A new species *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.** is described. All three new species were collected in one stream in Peruvian Amazonia.

РЕЗЮМЕ. Таксон Hagenulus/fg1 (или триба Hagenulini Kluge, 1994) в новом понимании включает неотропические таксоны Hagenulus/fg2, Hermanella/fg1, Thraulodes/g1, Ulmeritus/g1, Miroculis/g1; он характеризуется полной утратой пателло-тибиального шва на всех ногах и у личинки, и у имаго. Выделен новый таксон Hermanellonota **taxon n.**, или Hermanella/fg1 (возможное ранговое название — подтриба Hermanellina **subtr.n.**); он характеризуется двумя уникальными аутапоморфиями в строении гениталий самца и субимагинального мезонотума. Hermanellonota включает *Farrodes*, Simothraulopsis/g1 и Hermanellognatha. В составе Simothaulopsis/g1 выделен новый таксон *Maculognathus* **subgen.n.** (который можно считать подродом в роде *Simothaulopsis*) с двумя новыми видами — *Simothraulopsis* (*Maculognathus*) *sabalo* Kluge **sp.n.** и *S.*(*M.*) *plesius* Kluge **sp.n.** Hermanellognatha **taxon n.**, или Hermanella/fg2 (возможное ранговое название — род *Hermanella* s.l.) характеризуется уникальным ротовым аппаратом и некоторыми другими личиночными признаками. Описан новый вид *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**. Все три новых вида были собраны в одном ручье в перуанской Амазонии.

Printed in 2008.

Introduction

Recently it is used to divide the family Leptophlebiidae (which includes only 675 nominal species, including all synonyms and nomina dubia) into 140 genera, so that many of these genera are monospecific. Original descriptions of most genera are hardly understandable, because each consists of a list of characters repeated

several times — once as a simple description, next time supplied with statement, that this genus "can be separated from all other genera by the following combination of characters ..." (without concrete comparison with concrete genera), and so on. While among the characters described there are many important ones (larval mouthparts structure, shape of tergalii, imaginal wing venation and genital structure) some important characters were never described — particularly, presence of patella-tibial suture on middle and/or hind legs of larvae and/or adults, structure of subimaginal mesonotum, larval and subimaginal male genitals. Significance of these characters for characteristics of some high-level taxa was demonstrated in my earlier papers [Kluge, 1994a, 1994b]. It is also important to remember that no one character can be associated with a certain rank, generally speaking, but has significance only applying to a certain taxon. Some authors think that if one genus is characterized by a certain character, the same character should be regarded as generic in all other cases, and any species which differ by this character, should be placed to different genera. This error leads to endless splitting genera, as a result of which many genera become monospecific, i.e. genera become identical to species and, thus, lose their significance.

While there are established many genera, macrosystem of Leptophlebiidae is poorly elaborated. W.L. Peters [1980] established a large subfamily Atalophlebiinae and suggested that in future this subfamily should be divided into several tribes. Since that time only one tribe Hagenulini was suggested [Kluge, 1994a]; definition of this tribe was based on examination of Cuban representatives only, and did not take into account other Neotropical representatives, which were described incompletely. In the present paper this tribe is redefined basing on examination, besides Cuban, also Peruvian and some other species.

When artificial taxa are substituted by natural ones (permanent holophyla and temporary plesiomorphons), traditional ranks become inappropriate for them, because a limited number of ranks (subgenus, genus, subtribe, tribe, subfamily, family, etc.) is not enough to supply with ranks all natural taxa. Among all suggested nomenclatural systems, only the system of hierarchical and circumscriptional names allows to dissolve this problem in agreement with the existent zoological nomenclature regulated by the ICZN [Kluge, 1999]. This nomenclatural system was used in the revised system of Ephemeroptera other than Baetidae s.str. and Leptophlebiidae [Kluge, 2004]. In the present paper this nomenclatural system is applied for the discussed leptophlebiid taxa.

In the lists of material examined, the following arbitrary signs are used: **I** — imago; **S** — subimago; **L** — larva; **L-S** — subimago reared from larva (with larval exuviae); **S-I** — imago reared from subimago (with subimaginal exuviae); **L-S-I** — imago reared from larva (with larval and subimaginal exuviae).

Phylogeny and classification

Phylogenetic reconstruction should be based not on occasional combinations of characters (as in some calculations based on the non-scientific principle of parsimony), but on unique and conservative autapomorphies.

Overwhelming majority of Atalophlebiinae have the following features in mouthpart structure, not found in other taxa: maxilla lacks canines and has a single comb-like dentiseta directed apically; hypopharynx bears a pair of processes. These features are highly conservative, being retained in representatives with variously modified mouth apparates, independently of shape and specialization of maxillae and hypopharynx. The following phylogenetic hypothesis is based on assumption that each of these characters appeared once and just after its appearance became conservative:

The holophylum Leptophlebia/fg1 (corresponding to the family Leptophlebiidae in the generally accepted sense) is divided into (1) plesiomorphon Leptophlebia/fg2 (incl. *Paraleptophlebia*, *Neoleptophlebia*, *Habrophlebiodes*) and (2) holophylum Atalophlebia/fg1.

The holophylum Atalophlebia/fg1 is characterized by an autapomorphy — loss of maxillary canines. It is divided into (1) monospecific taxon *Calliarcys* and (2) holophylum Atalophlebia/fg2.

The holophylum Atalophlebia/fg2 is characterized by autapomorphies — comb-like form of the proximal dentiseta [Kluge, 1994b: Fig. 8; 2004: Fig. 106H] and transverse setal rows on labrum. It is divided into (1) holophylum Habrophlebia/fg1 (corresponding to the subfamily Habrophlebiinae Kluge, 1994) and (2) holophylum Atalophlebia/fg3 (corresponding to the subfamily Atalophlebiinae Peters 1980).

The holophylum Atalophlebia/fg3 is characterized by autapomorphies — square facets of upper portion of male eyes [Peters & Gillies, 1995] and loss of stout setae on distal margin of labrum. It is divided into (1) holophylum Terpides/g1 (corresponding to "*Terpides* lineage" by Savage, 1986) and (2) holophylum Atalophlebia/fg4.

The holophylum Atalophlebia/fg4 is characterized by an autapomorphy — loss of the distal dentiseta. So maxilla, instead of initial three canines and two dentisetae, has a single comb-like dentiseta directed apically (which corresponds to the initial proximal dentiseta); in a few taxa, such as Hermanellognatha (see below) and *Choroterpides*, this dentiseta is also lost. Atalophlebia/fg4 is divided into (1) *Castanophlebia* (with two African species) and (2) holophylum Atalophlebia/fg5.

The holophylum Atalophlebia/fg5 is characterized by an autapomorphy — presence of lateral processes on hypopharynx. It includes majority of Leptophlebiidae and has world-wide distribution.

Phylogeny of Atalophlebia/fg5 is not quite clear yet, because many taxa are described incompletely and material on them was not examined by me. Here belong Arctogean taxa Thraulus/g1 and Choroterpes/g1 (incl. *Choroterpides*, *Euthraulus*, *Neochoroterpes* et al.); Neotropical taxon Hagenulus/fg1 (see below) and taxa of Notogean origin. Below, only the taxon Hagenulus/fg1 is discussed.

1. Hagenulus/fg1

Hierarchical name: Hagenulus/fg1 (incl. *Thraulodes*, *Ulmeritus*, *Miroculis*, *Hermanella*) [f: Hagenulini Kluge, 1994; g: *Hagenulus* Eaton, 1882].

Possible ranking name: tribe Hagenulini Kluge, 1994 (redefined).

Autapomorphy of Hagenulus/fg1. Patella-tibial suture is lost on all legs of all stages — larva, subimago and imago (Figs 3, 7).

Most investigators of mayflies do not understand this character, thus it needs some comments. Initially mayflies have patella-tibial suture expressed on middle and hind legs, but reduced on fore legs; in some taxa it is reduced also on middle and/or hind legs; in two mayfly taxa it is secondarily restored on fore legs [Kluge, 2004]. When patella-tibial suture is expressed on larval leg, it represents an oblique groove which forms an ellipse or a part of ellipse, crossing at least inner side of tibia (Fig. 2). When this suture is expressed in adults (subimago and imago), it represents a concavity, which obliquely crosses inner side of tibia (Fig. 1). This character is very convenient for practical determination of larvae and adults, and should be used in keys.

This character is conservative in this lineage, but not unique. Among Leptophlebiidae, patella-tibial suture is lost on larval middle and fore legs, besides Hagenulus/fg1, in some other taxa, particularly in Choroterpes/g1 (including *Choroterpides*, *Euthraulus*, et al.), Thraulus/g1 and others. In these cases patella-tibial suture is lost only on larval legs, but is well-expressed on subimaginal and imaginal legs. Unlike them, in Hagenulus/fg1 patella-tibial suture is lost not only on larval, but on subimaginal and imaginal legs as well. Such loss of patella-tibial suture in all stages independently took place in some other taxa of Ephemeroptera [Kluge, 2004: Index of characters (1.2.17) and (2.2.82)]. But the assumption that American Leptophlebiidae possessing this character constitute a holophylum, does not contradict any other recently known facts.

Character of Hagenulus/fg1 of unclear phylogenetic status. Hind wing has more or less prominent costal projection; vein Sc terminates on costal margin just distad of costal projection, far from wing apex. The same in some other taxa, some of which have possible relationship with Hagenulus/fg1 (e.g. Choroterpes/g1, Thraulus/g1), and some are evidently non-related (e.g. Terpides/g1).

Plesiomorphy of Hagenulus/fg1. Imaginal and subimaginal claws are ephemeropteroid (unlike pointed in Terpides/g1 and some taxa of Notogean origin).

DISTRIBUTION. New World, dominate in Neotropical Region.

COMPOSITION. Hagenulus/fg1 (or thribe Hagenulini) includes the following subordinated taxa: (1) Hagenulus/fg2 (incl. *Borinquena*, *Turquinophlebia*, *Poecilophlebia*, *Careospina*, *Traverina*, *Hagenulopsis*, *Neohagenulus*) (= genus *Hagenulus* sensu Kluge, 1994); (2) Thraulodes/g1 (= genus *Thraulodes* in the recently accepted sense); (3) Ulmeritus/g1 (incl. *Ulmeritoides*) (= genus *Ulmeritus* sensu Traver, 1959); (4) Miroculis/g1 (probably corresponding "*Miroculis* lineage" sensu Savage & Peters, 1983); (5) Hermanellonota (see below). Some representatives of these taxa were examined by me, so it is known that they have no patella-tibial suture both in larvae and adults. *Askola* and *Atopophlebia* have no patella-tibial suture at least in larval stage (examined by me); possibly, they also belong to Hagenulus/fg1. Possibly, to Hagenulus/fg1 should be added some other Neotropical taxa, for which leg structure remained to be unknown.

Below, only the taxon Hermanellonota is discussed.

1.1. Hermanellonota, or Hermanella/fg1

Circumscriptional name: Hermanellonota, **taxon n**.

Hierarchical name: Hermanella/fg1 (incl. *Simothraulopsis*, *Farrodes*) [f: Hermanellina, **subtribus n**.; g: *Hermanella* Needham & Murphy, 1924].

Possible ranking name: subtribe Hermanellina, subtribus nov. (type genus *Hermanella* Needham & Murphy, 1924).

Unique autapomorphies of Hermanellonota.

(1) Cuticle of subimaginal mesonotum lost pigmented areas characteristic for other Leptophlebiidae [Kluge, 2004: Leptophlebia/fg1 (2)]; medioparapsidal suture, being not surrounded by the pigmented area, in its posterior part does not become shallower and reaches median suture; parascutellum is directly connected with lateroscutum, without membranous area between them. Unique apomorphy. In most species mesonotal cuticle is non-pigmented [Kluge, 1994a: Fig. 13; 2004: Fig. 106E]; in species with well-pigmented subimaginal mesonotal cuticle (among species examined this is *saltensis* [*Hydrosmilodon*]) its colour pattern sharply differs from all other Leptophlebiidae: medioparapsidal suture represent a colourless stripe, bordered by pigmented mediosscutum and pigmented submedioscutum (Fig. 29).

In some leptophlebiid species, not belonging to Hermanellonota, mesonotal subimaginal cuticle can be colourless, so they can be confused with Hermanellonota; these species can be distinguished from Hermanellonota if observe their translucent subimaginal exuviae at various kinds of light: at some light there are visible outlines of areas corresponding to the pigmented areas initial for Leptophlebiidae, while in Hermanellonota these areas are absent completely and can not be seen at any light.

(2) Each of two penial apices is produced into a slender sclerotized tubular process — **telopenis**, inside which the seminal duct passes. In imago these telopenes are sharply bent at their bases, being directed not caudally, but either laterally (in *Farrodes*), or even anteriorly, i.e. toward penis base (in *Simothraulopsis* and Hermanellognatha). Unlike imago, in mature larva telopenes represent apical continuations of penis lobes, being directed caudally, so that gonopores occupy apical position; larval penis itself (i.e. protopenis) can have developed gonopores with ducts lined by larval cuticle (Figs 10, 15, 32, 34). In subimago telopenes can occupy a position intermediate between the larval and the imaginal ones (Figs 12, 17). In subimago telopenes are sclerotized, while the rest penis can be membranous.

Among Hermanellonota, such telopenes with apical gonopores occur in *Simothraulopsis* and Hermanellognatha. In *Farrodes* telopenes can lack gonoducts, and gonopores can locate at their bases, that is a secondary condition (see below).

Telopenes can be confused with superficially similar processes, which occur in some other taxa (Habrophlebia/fg1, some Leptophlebia/fg2 et al.) and stretch from penis apex toward its base; but unlike telopenes, such processes do not bear the genital duct and do not change their direction during metamorphosis.

Other characters of Hermanellonota. Glossae are small, not curved ventrally (unlike Miroculis/fg1 and some others). On fore wing fork of MA is asymmetric (plesiomorphy in Leptophlebiidae). In cubital field of fore wing anteriormost of two intercalaries is either basally connected with CuA (Figs 20, 24, 30), or free (Fig. 14), but never connected with CuP (unlike Hagenulus/fg2).

DISTRIBUTION. The same as for Hagenulus/fg1 — New World, dominating in Neotropical Region.

DISCUSSION. The taxon Hermanellonota includes genera *Simothraulopsis*, *Farrodes* and the taxon Hermanellog-

natha (see below). Besides them, here probably belongs the genus *Homothraulus* Demoulin, 1955, which is recently restricted to the type species and two poorly known species more (Dominguez et al., 2006); imaginal and subimaginal genitals of these species, at least externally, are similar to that of *Simothraulopsis*. By shape of adult genitals, *Simothraulopsis* has also similarity with *Ecuaphlebia* Dominguez, 1988 — the genus established for two poorly known species [Dominguez, 1988; Dominguez et al., 2006]. Unlike the taxa included here into Hermanellonota, *Ecuaphlebia* has anterior cubital intercalary basally attached to CuP, that is characteristic for Hagenulus/fg2.

The genera *Homothraulus*, *Simothraulopsis* and *Farrodes* were united by Savage [1987] to the "*Farrodes*-group", which was later renamed to "*Homothraulus*-group", basing on the older generic name [Dominguez et al., 1997]. Probably, this group represents a plesiomorphon within Hermanellonota.

1.1.1. Simothraulopsis/g1

Hierarchical name: Simothraulopsis/g1 (incl. *Maculognathus*) [g: *Simothraulopsis* Demoulin, 1966].

Possible ranking name: genus *Simothraulopsis* Demoulin, 1966.

Autapomorphies.

(1) Hind wing has characteristic colour pattern (Fig. 21): costal margin blackish; posterior part usually brown. Shape of hind wing is constant: diminished, with prominent costal projection behind the middle, Sc terminates just behind costal projection, from its end a single constant cross-vein arises to RA. Larval hind protopteron has the same blackish stripe on costal margin, as in adults, but has no pigmentation of posterior part (Fig. 22).

(2) Male imaginal (but not larval) abdomen has characteristic colour pattern: each tergite II–V has translucent anterior part and brown posterior part, terga VI–IX are entirely brown [Dominguez et al., 1997: Figs 10–11]. Tergite I is dark brown in all stages — imago, subimago and larva.

Plesiomorphies and variable characters. Mouth apparatus is non-modified (unlike Hermanellognatha). Each tergalius has both lamellae lanceolately widened (Fig. 5) (unlike *Farrodes*). Lateral angles of styliger are projected posteriorly (unlike Hermanellognatha), but not so prominent as in *Farrodes*.

Penis has structure initial for Hermanellonota (see above): In imago and subimago gonoducts pass inside telopenes and open near their apices; imaginal telopenes are bent toward penis base (Fig. 13, 18–19). At least in *Maculognathus* larval protopenis represents a pair of simple-shaped, triangular-roundish lobes (unlike pointed lobes in *Hermanella chimaera* **sp.n.** and divergent lobes in *Farrodes*); each lobe has a roundish gonopore on its ventral side near apex, from which arises a gonoduct lined by larval cuticle (Figs 10, 15) (unlike closed gonopore in *Farrodes*).

On fore wing MA forms an asymmetric fork; MP varies from symmetrically forked to unforked with independent MP_2. This variation of MP was wrongly interpreted as "developmental change" [Dominguez et al., 1997: 146]; actually all insects have shape of veins unchangeable during development from larval protopteron to imaginal wing [Kluge, 2000]. Among the two species described below, in *S. (M.) sabalo* **sp.n.** vein MP varies from symmetrically forked (Fig. 14) to asymmetrically forked, and in *S. (M.) plesius* **sp.n.** — from asymmetrically forked (Fig. 24) to unforked (Fig. 20).

DISCUSSION. The original description of the genus *Simothraulopsis* and its type species *S. surinamensis* was based on six immature larvae [Demoulin, 1966]. Dominguez et al. [1997] synonymized *S. surinamensis* with *Thraulus demerara* Traver, 1947 and redescribed the genus *Simothraulopsis* and species *S. demerara*, basing on the type specimens of *T. demerara* and additional material, but without reexamination of the types of *S. surinamensis*. In the original description of *S. surinamensis*, there is a figure of larval hind protopteron [Demoulin, 1966: Fig. 9m], on which two equally short crossveins arise from Sc to RA. Unlike this, mayflies recently ascribed to *Simothraulopsis*, have a single long constant crossvein arising from apex of Sc to RA [Figs 21–22; Dominguez et al., 1997: Figs 3–5; Traver, 1947: Fig. 5]. Possibly, the Demoulin's figure contains errors connected with indistinct outlines of veins in larval protopteron. Here I accept interpretation of *Simothraulopsis* by Dominguez et al. [1997], but in order to confirm its correctness, it would be useful to reexamine the Demoulin's type material.

COMPOSITION. Till now, the genus *Simothraulopsis* included a single species *Thraulus demerara* Traver, 1947 (= *Simothraulopsis surinamensis* Demoulin, 1966); larvae, subimagines and imagines of this species are described by Traver [1947], Demoulin [1966] and Dominguez et al. [1997]. In the present paper two other species are described — *S. sabalo* and *S. plesius* **spp.n.** Both these species have just the same colour pattern of imaginal abdomen and hind wing, as in *S. demerara*, that indicates their relationship and allows to place them into the same genus. The two new species, besides this, have common unique features in colour of larval cuticle and imaginal legs, that indicated their especially close relationship and allows to unite them into a new subgenus *Maculognathus* (see below). At the same time, larva of *S. plesius* Kluge **sp.n.** differs from two other species of *Simothraulopsis* (and from all other Hermanellini) by possessing posterolateral spines on abdominal segment VII. The former diagnosis of *Simothraulopsis* included such character as presence of larval posterolateral spines on VIII–IX abdominal segments only [Demoulin, 1966; Dominguez et al., 1997; Dominguez et al., 2006]; now this character is excluded from the general diagnosis of *Simothraulopsis* s.l.

1.1.1.1. Simothraulopsis/g2

Hierarchical name: Simothraulopsis/g2 (sine *Maculognathus*).

Possible ranking name: subgenus *Simothraulopsis* Demoulin, 1966.

Includes a single described species *Simothraulopsis* (*Simothraulopsis*) *demerara* (Traver, 1947 [*Thraulus*]) (= *Simothraulopsis surinamensis* Demoulin, 1966) (see above).

1.1.1.2. Maculognathus/g(1)

Hierarchical name: Maculognathus/g(1) [g: *Maculognathus* subgen.n.]

Possible ranking name: subgenus *Maculognathus* **subgen.n.**

Type species: *Simothraulopsis* (*Maculognathus*) *plesius* **sp.n.**

Autapomorphies.

(1) In larva, on exposed side of each mandible, cuticle is pigmented, with a distinctly outlined colourless blank (Figs 4, 25). Such blank is found in some other taxa, but not in *S. demerara* [Dominguez et al., 1997: Fig. 16].

(2) In imago and subimago femora have following peculiar brown and whitish pattern: on fore femur only apical-inner part is whitish; on middle and hind femur basal-outer and apical-inner parts are whitish, so brown area looks like a large oblique band (Fig. 3) (unlike *S. demerara*, whose femora have brown subapical bands only).

General characteristic. The both species of *Maculognathus* have the following common characters in structure and coloration of larvae, subimago and imago.

Larva. Cuticular pigmentation: Head in most part is brown, with distinctly outlined contrasting colourless blanks:

all specimens have three blanks corresponding to three ocelli; in *S.*(*M.*) *plesius* **sp.n.** the blank corresponding to medial ocellus stretches anteriorly so that represents a wide medial stripe all along clypeus and labrum (Fig. 25). Antennae and their bases are colourless. Each mandible has exposed part dark brown with one distinctly outlines colourless blank (Figs 4, 25). Sometimes there are smaller blanks between ocelli. Stipes of each maxilla is dark laterally, other mouth-parts are light. Pronotum and mesonotum are brown, can be lighter than head, with distinct or diffusive blanks of composite shape; fore protopteron with diffusive darker stripes corresponding to convex veins of wing. Fore femur with wide subapical brown band and wide zigzag middle brown band, other parts are colourless (Fig. 6). Middle femur with the same subapical band; its middle zigzag band is widened and expanded proximally; proximal light area with darkened margins. On hind femur both transverse bands and proximal darkenings are fused, so femur in is most part brown, with several colourless blanks and colourless apex. On all legs tibiae and tarsi have alternating brown and colourless areas: tibia has two brown bands — at base and behind middle, being colourless at middle and at apex; tarsus has one dark band, being colourless at extreme base and behind middle (Fig. 6). Abdominal terga are light brown, sometimes with unpaired and/or paired blanks varying from tergite to tergite and among specimens. Caudalii are either uniformly coloured, or with each second segment lighter.

Hypodermal pigmentation: Hypoderm of head, pronotum, mesonotum and abdominal terga with dark gray ornament, which partly coincides, partly contradicts cuticular pigmentation; on head and mandibles blanks of hypoderm coincide with characteristic blanks of cuticle (see above). Hypoderm of hind protopteron has the same dark gray stripe at costal margin, as on imaginal wing (Fig. 22); the rest part of protopteron is unicolour, without posterior darkening characteristic for imaginal wing. Legs of young larva have hypoderm nearly colourless, so their colour is determined by cuticle (see above); in larva of last instar legs get hypodermal colour of adult type, which does not agree with larval cuticular colour pattern. Hypodermal colour pattern of larval abdominal terga is variable; it can include various dark and light gray paired maculae, separated or not separated by blanks; sometimes there are unpaired median blanks on all or some segments; even in mature larva it can be quite different from imaginal colour pattern (which is more uniform and never has median blanks — see below).

Mouth apparatus: as described for *Simothraulopsis* [Dominguez et al., 1997].

Leg setation: Fore femur with irregularly situated long and short blunt stout setae on distal half of outer margin; a few such setae on distal half of dorsal surface form an oblique row stretching from middle of outer margin to apex of inner margin; most surface and inner margin without setae (Fig. 6). Fore tibia on inner side bears dense irregularly situated short spine-like pointed bipectinate setae; close to them, but more ventrally, locates a regular row of lighter pointed bipectinate setae of the same size; distalmost of these lighter setae is twice longer than others. Middle femur with irregularly situated long and short blunt stout setae on distal half of outer margin; shorter setae of such kind all along dorsal surface and on distal half of inner margin. Middle tibia with a few spine-like bipectinate setae on inner side and a longitudinal row of short blunt setae on dorsal (anterior) side. Hind femur with irregularly situated long and short blunt stout setae all along outer margin; shorter setae of such kind all along dorsal surface and on distal half of inner margin. Hind tibia with a sparse longitudinal row of spine-like bipectinate setae on inner side, a longitudinal row of stout blunt setae on dorsal (anterior) side, a sparse row of long pointed bipectinate light setae on ventral (posterior) side, and a longitudinal row of small stout blunt setae on outer side; apex on ventral side with transverse row of pectinate spine-like setae (Fig. 7). Besides these stout setae, there are sparse long hair-like setae on outer margins of femora, tibiae and tarsi of all legs (not shown in Figs 6 and 7).

Claws: On each leg claw with one row of denticles, with the distalmost denticle much larger than others; in other respects shape of claws is differs in *S.*(*M.*) *sabalo* and *S.*(*M.*) *plesius* **sp.n.** (see below; Figs 8, 16).

Abdomen: Posterior margin of sternum IX in female convex, with small shallow median incision; in male with protogonostyli brought together (Figs 9, 15). Posterolateral spines are differently developed in *S.*(*M.*) *sabalo* and *S.*(*M.*) *plesius* **sp.n.** (see below).

Tergalii: All tergalii I–VII are bilamellate, with each lamella lanceolate (Fig. 5).

Subimago. Subimaginal cuticle is colourless [about structure of mesonotum — see Hermanellonota (1) above]. Thorax with dark gray hypodermal maculation, sterna are lighter; in young subimago mesonotum is whitish (unlike brown in imago). Hypodermal pigmentation of legs and abdomen as in imago.

Male imago. Upper portion of eye is low, reddish; lower portion is gray. Thorax is dark brown, with sterna lighter. On fore leg femur in most part is brown, apical area adjacent to inner margin is whitish; tibia has proximal half brown, distal half whitish; tarsus is entirely whitish. On middle and hind legs femur is in most part brown, outer-basal and inner-apical areas are whitish; tibia (lacking patella-tibial suture — see Hagenulus/fg1 above) is dark brown except for extreme apex; apex of tibia and entire tarsus (including first segment fused with tibia) are whitish (Fig. 3). Fore wing with base brown, other part colourless, veins pale. Hind wing with costal area blackish (pigmentation retaining from larval protopteron). Posterior part of hind wing is more or less coloured by brown; brown area occupies either half of wing (Fig. 21), or a smaller area adjacent to posterior margin. Abdominal tergite I is brown; each tergite II–V is whitish anteriorly and dark brown posteriorly; terga VI–IX are entirely dark brown; tergite X is whitish, with brown maculae. Abdominal sternite I is whitish; each sterna II–IV are whitish with a pair of lateral brown spots, sterna V–IX in most part brown. Styliger, gonostyli and penis are brown; shape of gonostyli and penes somewhat differ in *S.* (*M.*) *sabalo* and *S.* (*M.*) *plesius* **spp.n.** (see below). Caudalii are proximally dark brown, distally whitish.

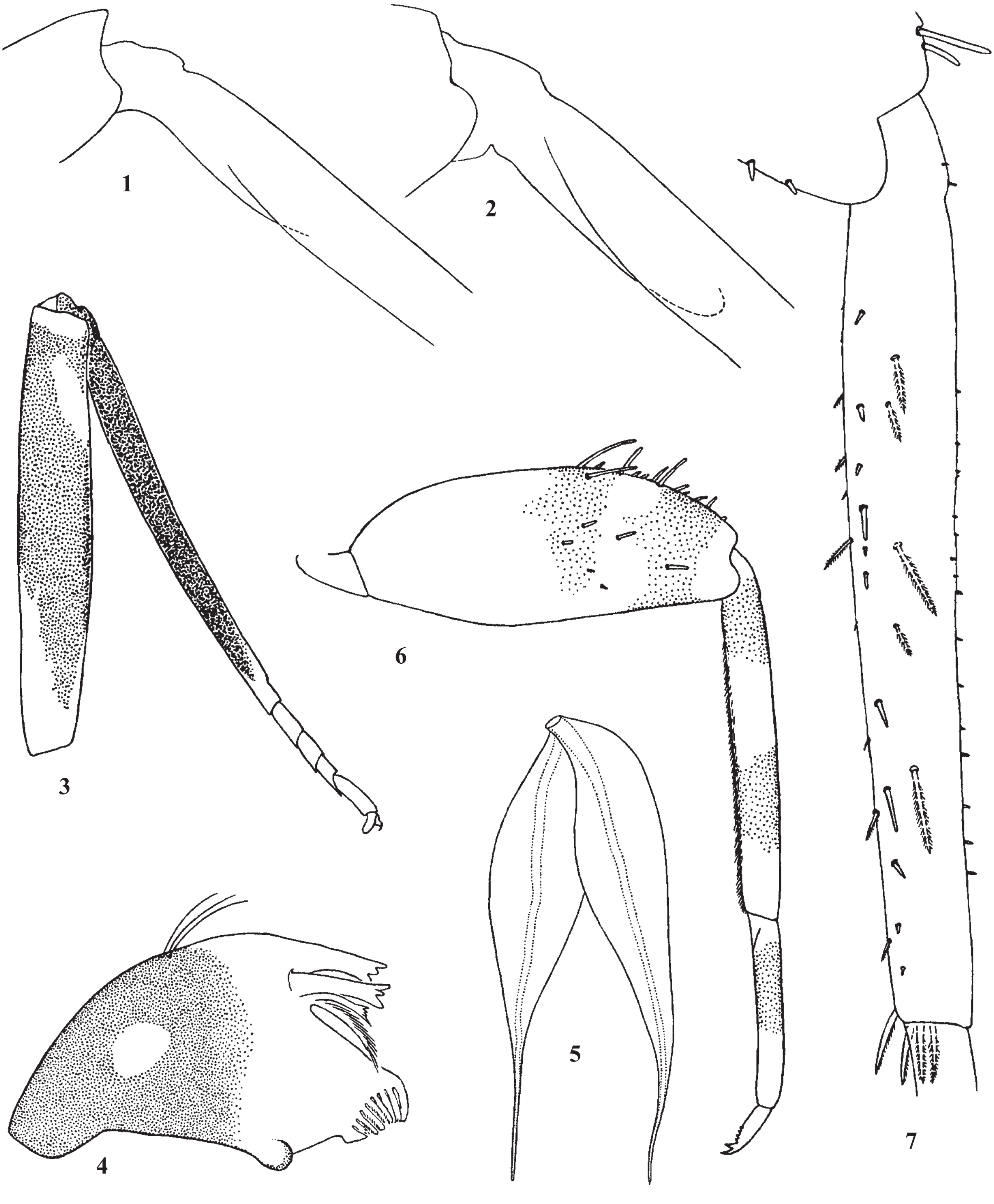
Female imago. Colour is similar to male, but abdominal terga have brown areas larger, sometimes entirely brown.

COMPOSITION. The taxon *Maculognathus* includes 2 species — *Simothraulopsis* (*Maculognathus*) *sabalo* and *S.*(*M.*) *plesius* **spp.n.**, which were collected in the same locality in Peruvian Amazonia.

1.1.1.2.a. ***Simothraulopsis*** **(*Maculognathus*)** ***sabalo*** Kluge **sp.n.** Figs 3–14.

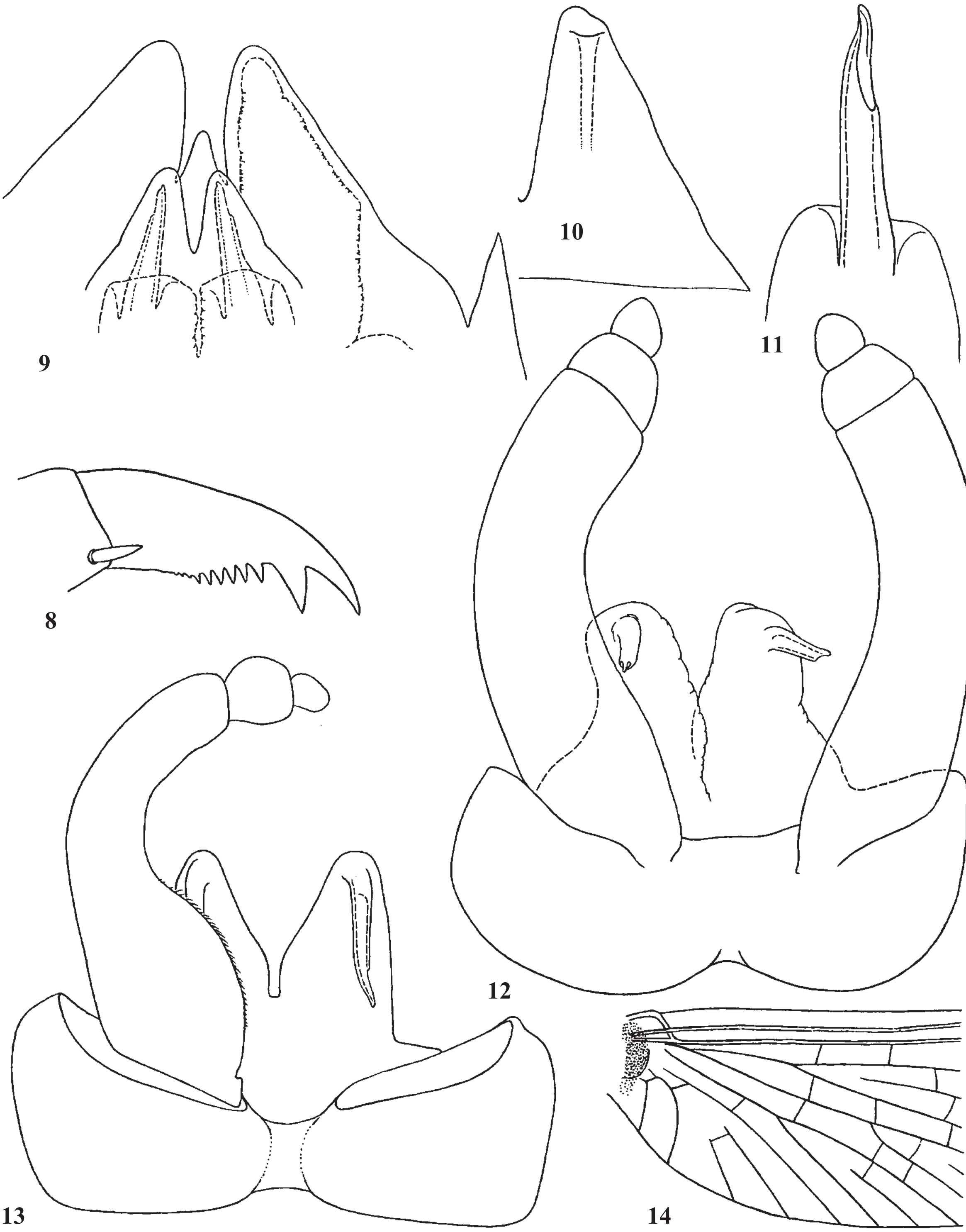
MATERIAL EXAMINED. PERU, Prov. LORETO: Quebrada El Sabalo, right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 1–16.II.2006 (N. Kluge) — 1 L-S-I♂ (holotype, 11.II.2006), 11 L-S♂, 1 S-I♂, 1 L-S-I♀, 5 L-S♀, 24 L♂, 60 L♀.

Larva. Cuticular colour of most specimens is somewhat lighter than in *S.*(*M.*) *plesius* **sp.n.**, with blanks less contrast-



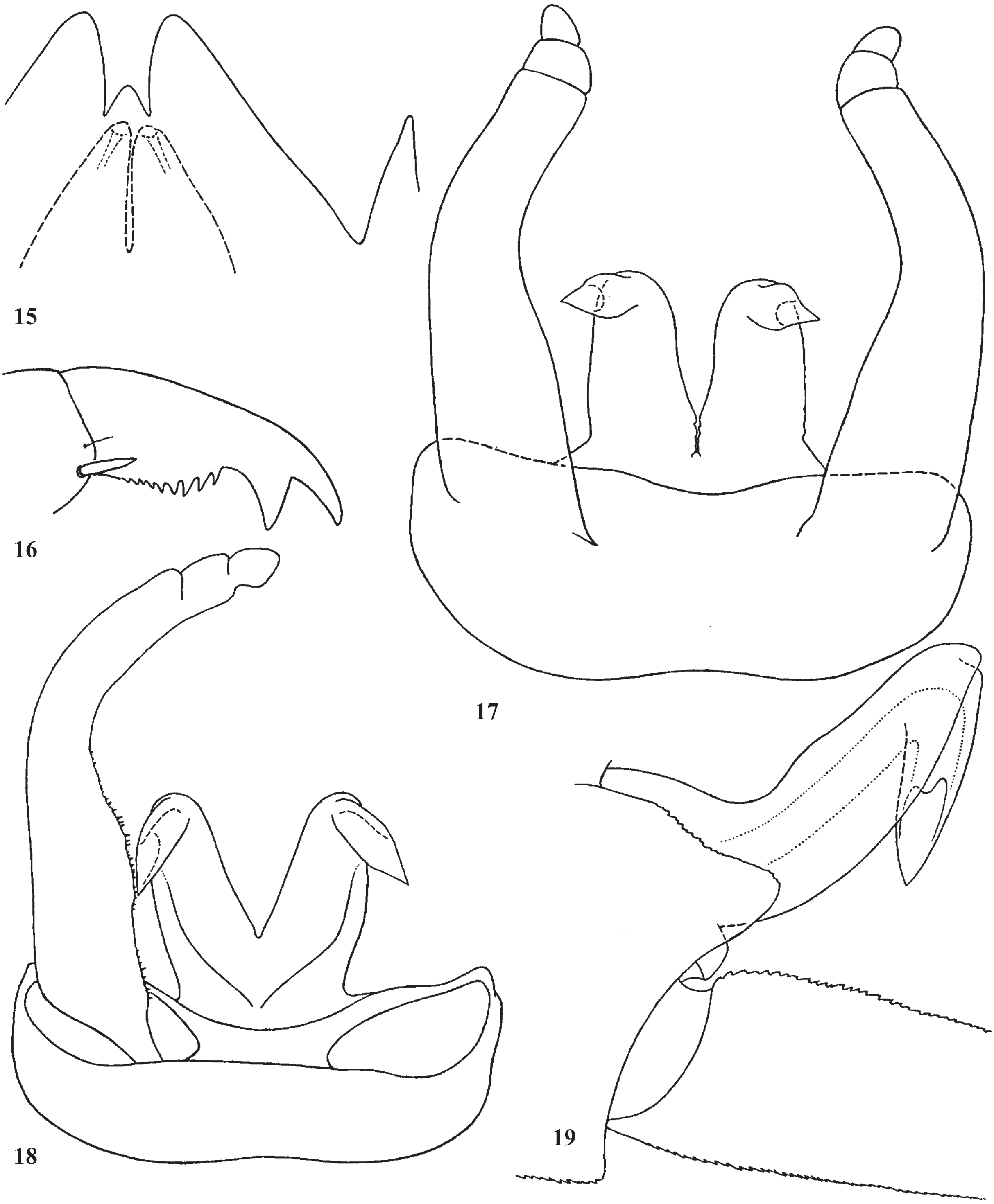
Figs 1–7: 1–2 — *Meridialaris tintinnabula*: 1 — proximal part of hind tibia, subimago; 2 — the same, larva; 3–7 — *Simothraulopsis* (*Maculognathus*) *sabalo* **sp.n.** (3, 4, 6, 7 — holotype): 3 — hind leg of imago; 4–7 — larva: 4 — left mandible; 5 — right tergalius III; 6 — fore leg (cuticular pigmentation shown by dots, hypodermal pigmentation not shown; long fine setae on outer margin of femur, tibia and tarsus not shown); 7 — tibia of hind leg (bipectinate setae on opposite side shown by interrupted line; long fine setae on outer margin not shown).

Рис. 1–7: 1–2 — *Meridialaris tintinnabula*: 1— проксимальная часть задней голени субимаго; 2 — то же, личинка; 3–7 — *Simothraulopsis* (*Maculognathus*) *sabalo* **sp.n.** (3, 4, 6, 7 — голотип): 3 — задняя нога имаго; 4–7 — личинка: 4 — левая мандибула; 5 — правая тергалия III пары; 6 — передняя нога (кутикулярная пигментация показана пунктировкой, гиподермальная пигментация не показана; длинные тонкие щетинки на наружном крае бедра, голени и лапки не показаны); 7 — голень задней ноги (двоякогребенчатые щетинки на противоположной стороне показаны прерывистой линией; длинные тонкие щетинки на наружном крае не показаны).



Figs 8–14. *Simothraulopsis* (*Maculognathus*) *sabalo* Kluge **sp.n.**: 8 — larval claw (holotype); 9–11 — genitals of mature male larva ready to moult to subimago: 9 — larval protopenis and protogonostyli, dorsal view (buds of subimaginal penis and one gonostylus shown by interrupted line); 10 — right lobe of larval protopenis, ventral view (cuticular larval gonoduct shown by interrupted line); 11 — bud of right lobe of subimaginal penis, extracted from larval protopenis, ventral view (cuticular subimaginal gonoduct shown by interrupted line); 12 — genitals of male subimago, ventral view; 13 — genitals of male imago, ventral view; 14 — proximal part of fore wing.

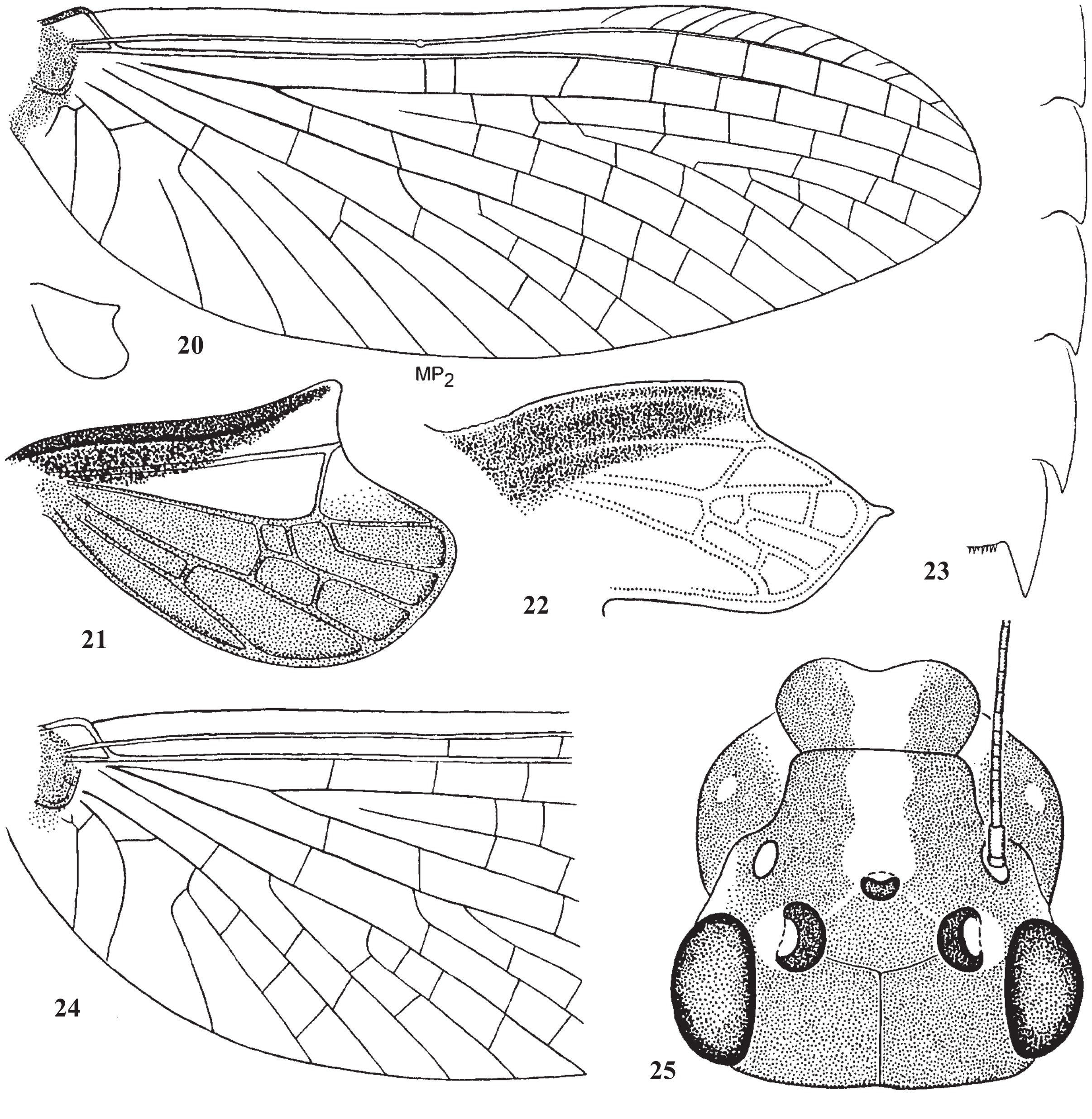
Рис. 8–14. *Simothraulopsis* (*Maculognathus*) *sabalo* Kluge **sp.n.**: 8 — коготок личинки (голотип); 9–11 — гениталии зрелой личинки самца, готовой к линьке на субимаго: 9 — протопенис и протогоностили личинки, дорсально (зачатки субимагинального пениса и одного гоностиля показаны прерывистой линией); 10 — правая доля личиночного протопениса, вентрально (кутикулярный личиночный гонодукт показан прерывистой линией); 11 — правая доля субимагинального пениса, отпрепарированная из личиночного протопениса, вентрально (кутикулярный субимагинальный гонодукт показан прерывистой линией); 12 — гениталии самца субимаго, вентрально; 13 — гениталии самца имаго, вентрально; 14 — проксимальная часть переднего крыла.



Figs 15–19. *Simothraulopsis* (*Maculognathus*) *plesius* Kluge **sp.n.**: 15 — genitals of mature male larva, ventral view (larval protopenis shown by interrupted line); 16 — larval claw; 17 — genitals of male subimago, ventral view; 18 — genitals of male imago, ventral view; 19 — the same, view from the left (gonoduct shown by dotted line).

Рис. 15–19. *Simothraulopsis* (*Maculognathus*) *plesius* Kluge **sp.n.**: 15 — гениталии зрелой личинки самца, вентрально (личиночный протопенис показан прерывистой линией); 16 — коготок личинки; 17 — гениталии самца субимаго, вентрально; 18 — гениталии самца имаго, вентрально; 19 — то же, вид слева (гонодукт показан пунктиром).

ing. Blank of median ocellus is roundish; labrum is either unicolour brown or lighter medially, but there is no integral blank stretching from median ocellus through entire clypeus and labrum. On each leg claw is slender; among denticles other than the distalmost one (which is much larger than others — see characteristics of *Maculognathus* above) the largest are distal ones (Fig. 8). Posterolateral spines present on abdominal segments VIII–IX only [unlike *S.* (*M.*) *plesius*



Figs 20–25. *Simothraulopsis* (*Maculognathus*) *plesius* Kluge **sp.n.**: 20 — fore and hind wings on the same scale; 21 — hind wing; 22 — larval hind protopteron; 23 — lateral margin of V–IX abdominal segments of larva (holotype); 24 — proximal part of fore wing; 25 — head of female larva (cuticular pigmentation shown by dots, hypodermal pigmentation not shown).

Рис. 20–25. *Simothraulopsis* (*Maculognathus*) *plesius* Kluge **sp.n.**: 20 — переднее и заднее крылья в одном масштабе; 21 — заднее крыло; 22 — задний протоптерон личинки; 23 — латеральный край V–IX сегментов брюшка личинки (голотип); 24 — проксимальная часть переднего крыла; 25 — голова личинки самки (кутикулярная пигментация показана пунктировкой, гиподермальная пигментация не показана).

sp.n., as in other Hermanellonota]. Other characters as described for *Maculognathus* (see above).

Male imago and subimago. On fore wing furcation of MP varies from symmetric (Fig. 14) to slightly asymmetric (similar to Fig. 24) — i.e. MP_2 is always attached to MP, and MP_1 forms some angle with common stem MP; at least among specimens examined, independent MP_2 is not found. Gonostyli of subimago and imago are sharply different: in subimago largest (1st+2nd) segment is evenly arched, parallel-sided, thick all over its length, without any difference between initial 1st and 2nd segments (Fig. 12); in imago proximal part of this segment (corresponding to initial 1st segment) is sharply swollen, thicker than in subimago, with convex inner margin, while distal part (corresponding to initial 2nd segment) is much thinner than in subimago (Fig. 13). Telopenes of subimago and imago have the same shape — narrow, nearly parallel-sided, with oblique subapical gonopore (Figs 9–13). Other characters as described for *Maculognathus* (see above).

Dimensions. Fore wing length (and approximate body lenght) 4.5–5 mm.

1.1.1.2.b. *Simothraulopsis* (*Maculognathus*) *plesius* Kluge **sp.n.** (Figs 15–25)

? = "Genus nr. *Atalonella* sp.1": Roback 1966

MATERIAL EXAMINED. PERU, Prov. LORETO: Quebrada El Sabalo, right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 1–16.II.2006 (N. Kluge) — 8 L-S♂ (among them holotype, 11.II.2006), 4 L-S-I♀, 2 L-I♀, 9 L-S♀, 2 I♂, 4 L♂, 29 L♀.

Larva. Cuticular colour of most specimens is darker than in *S.*(*M.*) *sabalo* **sp.n.**, with blanks more contrasting; clypeus and labrum always have a wide median blank all along their length (Fig. 25). On each leg claw is widened; among denticles other than the distalmost one (which is much larger than others — see characteristics of *Maculognathus* above) the largest are middle ones (Fig. 16). Posterolateral spines present on abdominal segments VII–IX (Fig. 23), sometimes on segments VI–IX or V–IX [unlike *S. (M.) sabalo* **sp.n.** and all other Hermanellonota, which have spines on segments VIII–IX only]. Other characters as described for *Maculognathus* (see above).

Male imago and subimago. On fore wing MP varies from non-furcate (Fig. 20) to asymmetrically furcate (Fig. 24) — i.e. $MP+MP_1$ is nearly straight, and MP_2 is either independent, or attached to $MP+MP_1$; at least among specimens examined, symmetric furcation of MP is not found. Gonostyli of subimago and imago are similar: the largest ($1^{st}+2^{nd}$) segment has proximal part (corresponding to initial 1st segment) rather long and thicker than distal part (corresponding to initial 2nd segment) (Figs 17–18). Telopenes of subimago and imago have the same shape — wide-lanceolate, widest in middle, with oblique subapical gonopore and pointed apex (Figs 17–19). Other characters as described for *Maculognathus* (see above).

Dimensions. Fore wing length (and approximate body lenght) 5.5 mm.

DISCUSSION. Roback [1966] described a single small (3.6 mm) immature female larva from river Nanay (a tributary of Amazon near Iquitos), which has "lateral spines on segments 6–9" and other characters similar to that of *S.(M.) plesius* **sp.n.** Possibly, it is the same species.

1.1.2. **Farrodes/g(1)**

Hierarchical name: Farrodes/g(1) [g: *Farrodes* Peters, 1971]

Possible ranking name: genus *Farrodes* Peters, 1971.

MATERIAL EXAMINED. *Farrodes bimaculatus* Peters, 1971 (Figs 27–28) [all stages; material examined is listed in Kluge, 1994a]; *Farrodes hyalinus* Peters, 1971 (Jamaica, male subimagoes); *Farrodes* sp. (Guatemala, male subimago extracted from larva); *Farrodes* sp. (Panama, male subimago and larva); *Farrodes pakitza* (see below).

Male genitals. In my previous paper about Neotropical Leptophlebiidae there is given a figure of genitals of mature male larva of *Farrodes bimaculatus* [Kluge, 1994: Fig. 3], which contains an error: apical parts of subimaginal penes are taken for larval protopenes, while true larval protopenes are not drawn. Actually larval protopenes have simple shape with apices rounded and somewhat divergent; concavities corresponding gonopores, are located apically-laterally-dorsally; unlike *Simothraulopsis*, they have no cuticular gonoducts. In mature larva subimaginal-imaginal telopenes developed under larval cuticle, are directed caudally with apices bent laterally-dorsally (Figs 27–28). After moult to subimago, telopenes turn laterally [Peters, 1971: Fig. 77]. The same structure of larval protopenis with divergent gonopores occurs in *Farrodes pakitza* and in an undetermined species from Guatemala; possibly, it is characteristic for *Farrodes* in general. As in other Hermanellonota, gonopores are located on apices of telopenes, which in *Farrodes* are directed laterally or laterally-dorsally; probably in some species in imago these primary gonopores are closed, and secondary gonopores are opened on bases of telopenes [Dominguez, 1999: Fig. 62].

Other characters of Farrodes are adequately described by Peters [1971] and Kluge [1994].

COMPOSITION. Recently there are described 22 species of *Farrodes*. Among them, only one species — *F. pakitza* — was found in Peru, where it inhabits quite divers areas — from Andes (Tingo Maria, Pichanaki) to Amazonian Lowland.

1.1.2.a. ***Farrodes pakitza*** Dominguez, Molineri & Peters, 1996 (Fig. 26)

? = "Genus nr. *Atalonella* sp.2": Roback, 1966.

MATERIAL EXAMINED. PERU: Prov. JUNIN: Rio Shima 16 km SE Puerto Ocopa, 6.I.2006 (A.Petrov) — 2 S♀; small tributary of Rio Sotorani (right tributary of Rio Perene lower Pichanaki), 6–11.I.2006 (N.Kluge) — 2 L-S♂, 3 L-S♀, 1 L♂, 11 L♀; Prov. HUANUCO: Tingo Maria, Puente Perez, Rio Cantaria, 22–25.I.2006 (N.Kluge) — 1 L-S-I♂, 2 L-S-I♀, 1 L♂; Prov. UCAYALI: Aguaytia, La Choza, left tributary of Rio Yurac, 22–26.II.2006 (N.Kluge) — 2 L-S-I♂, 1 L-S♂, 4 L-S♀, 1 I♂, 3 I♀, 1 S♂, 4 S♀, 7 L♂, 6 L♀; Prov. LORETO: Rio Itaya above Puente Itaya (57 km by road from Iquitos), 1–15.II.2006 (N.Kluge) — larval exuviae, 1 L♀; Quebrada El Sabalo (right tributary of Rio Itaya at midway between Puente Itaya and San Joaquin de Omaguas on Rio Amazon), 1–16.II.2006 (N. Kluge) — 2 L-S♂, 2 L-S♀, 28 I♂, 30 S♂, 2 I♀, 23 S♀, 3 L♂, 4 L♀.

Male imago. Fore and middle legs without hypodermal pigment, in imago and subimago uniformly light; hind legs with dark subapical band on femur. Abdomen with peculiar colour pattern: terga II–VI have uniform pattern of darker brown and lighter reddish-brown stripes as figured by Dominguez et al. (1996: Figs 41–42); tergite VII has similar colour pattern, bur with a large transverse whitish spot close to posterior margin (Fig. 26). In subimago dark parts are light brown, in imago — dark brown. Other characters as in original description.

Larva. Cuticular pigmentation: most of dorsum brownish, nearly unicolour, without contrasting blanks. Dorsal side of head only with light blanks corresponding to ocelli; mandibles with exposed parts pigmented, hidden parts colourless. Thorax without blanks and darkenings. Each leg light, femur with diffusive dark band near apex, tibia and tarsus with bands arranged as in *Simothraulopsis* (similar to Fig. 6). Anteriormost abdominal terga lighter, posteriormost darker; each tergum uniformly coloured, without blanks (unlike *F. bimaculatus*).

Dimensions. Fore wing length (and approximate body lenght) 3.5–4 mm.

DISCUSSION. Roback [1966] described larvae from rivers near Tingo Maria, which have characters of *Farrodes*. Possibly, it is the same species.

1.1.3. **Hermanellognatha**, or **Hermanella/fg2**

Circumscriptional name: Hermanellognatha, **taxon.n.**

Hierarchical name: Hermanella/fg2 (sine *Simothraulopsis*, *Farrodes*; incl. *Traverella*, *Leentvaaria*, *Needhamella*, *Hylister*)

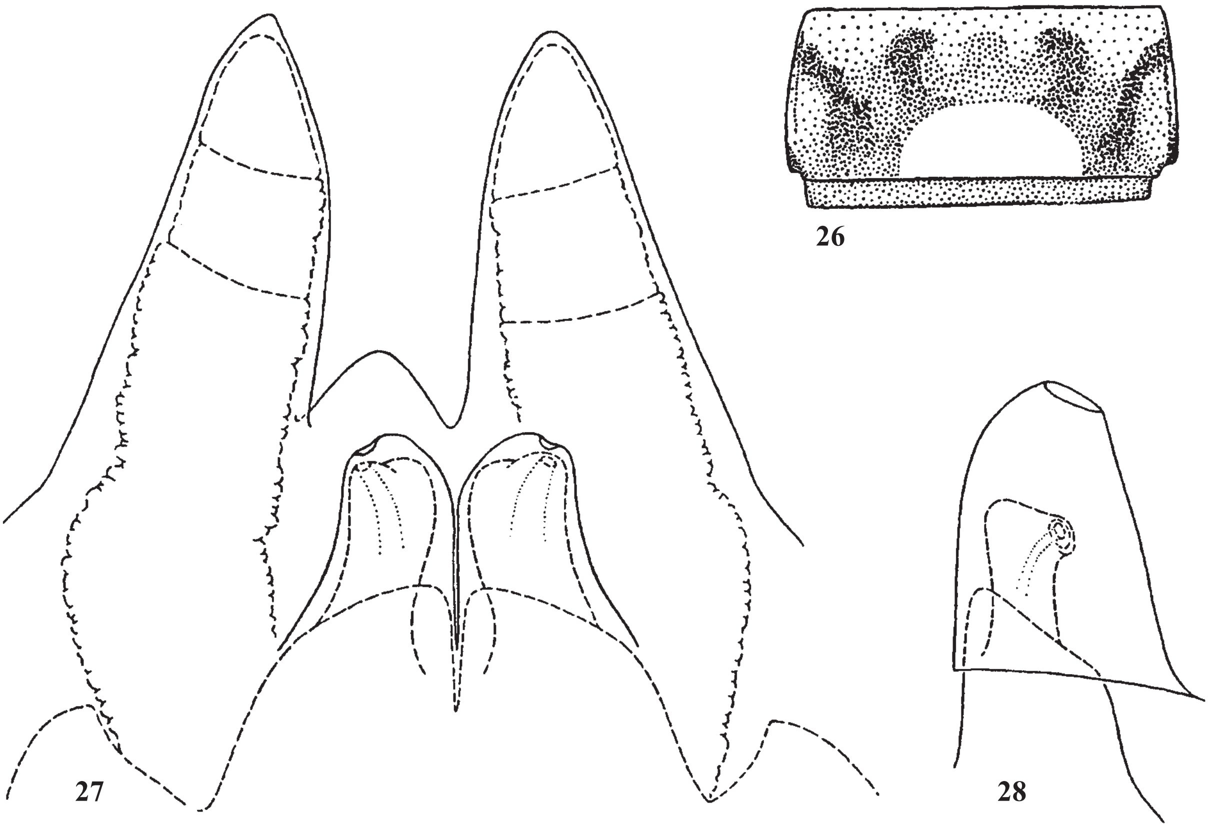
Possible ranking name: genus *Hermanella* Needham & Murphy, 1924 (s.l.).

= "*Hermanella* lineage": Savage, 1987

= "*Hermanella* complex": Dominguez & Flowers, 1989

Autapomorphies of Hermanellognatha.

(1) Mouth apparatus is specialized as filtering, with unique structure of maxillary palp. Stipes of maxilla is shortened, so maxillary palp is attached close to articulation with cardo; 1st segment of maxillary palp is enormously shortened, its length



Figs 26–28. *Farrodes* spp.: 26 — *F. pakitza*, abdominal tergite VII of male imago, spread on slide; 27–28 — *F. bimaculatus* from Cuba: 27 — genitals of mature male larva ready to moult to subimago, dorsal view (buds of subimaginal penis and gonostyli shown by interrupted line); 28 — a half of larval protopenis with bud of subimaginal penis just before moult to subimago, dorsal-median view.

Рис. 26–28 *Farrodes* spp.: 26 — *F. pakitza*, VII тергит брюшка самца имаго, расправленный на препарате; 27–28 — *F. bimaculatus* с Кубы: 27 — гениталии зрелой личинки самца, готовой линять на субимаго, дорсально (зачатки субимагинального пениса и гоностилей показаны прерывистой линией); 28 — половина личиночного протопениса с зачатком субимагинального пениса перед самой линькой на субимаго, вид с дорсально-медиальной стороны.

does not exceed width, outer side with characteristic stout clavate setae; 2nd segment is the longest; 3rd (distal) segment bears numerous long filtering setae arranged in several regular transverse rows; apex of this segment is produced into a long, pointed, soft process lacking setae (Fig. 37).

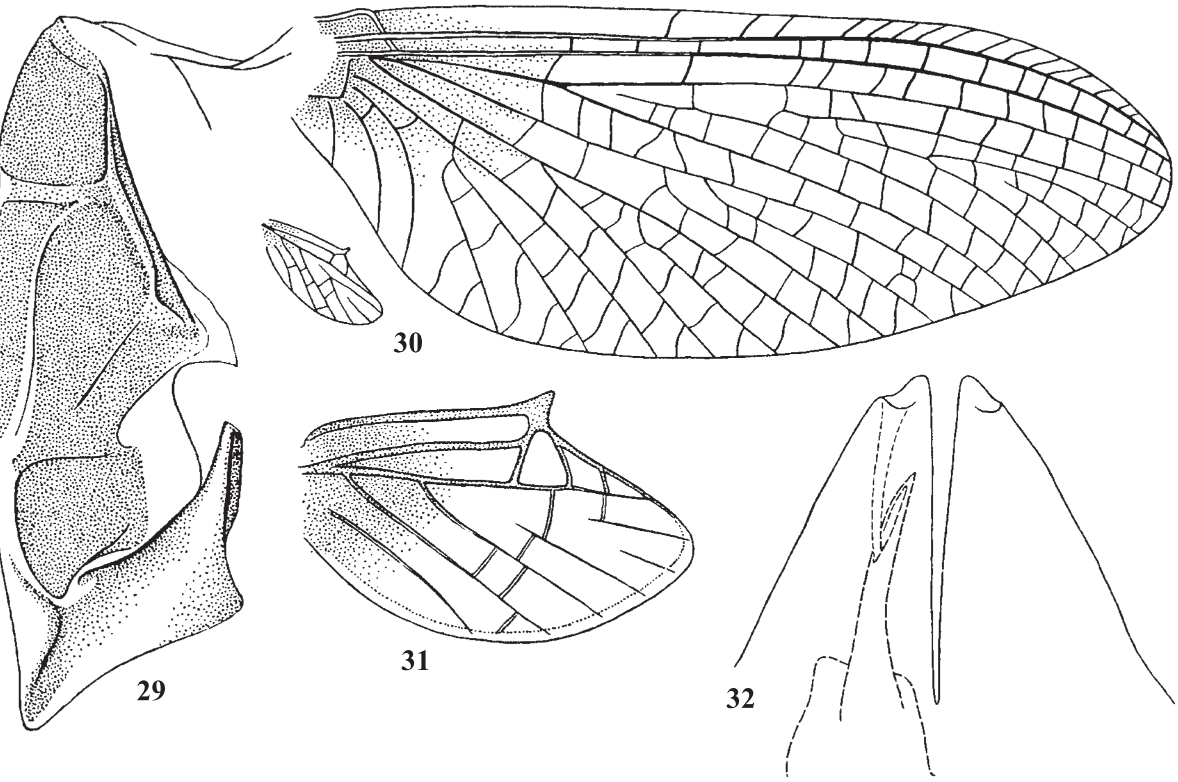
Other mouth parts (labrum, mandibles, superlinguae, hypopharynx, maxillae and paraglossae of labium) are strongly widened and modified. Clypeus is sharply widened distally in such a manner, that its lateral margins have unique concave shape (Figs 38–39). Labrum is strongly widened, wider than clypeus, with posterior margin straight, anterior margin convex; median emargination is narrowed and lost denticles; regular transverse row of long setae is shifted to proximal part of labrum and interrupted medially (Figs 38–39). Mandibles are flattened and widened, with outer margin angulate. Inner-apical angle of maxilla is produced to a tusk-like process (which can be from very small to huge — Fig. 37); single pectinate dentiseta (characteristic for Atalophlebia/fg4) and ventro-apical row of pectinate setae (characteristic for Leptophlebiidae in general) are completely lost.

Some of these features — widened labrum with setal row shifted basally and interrupted medially, widened superlinguae and hypopharynx, very long setae on maxillary palp and widened labium — independently evolved in other taxa with filtering specialization of mouth apparatus — the genus or subgenus *Hagenulus* s.str. (belonging to Hagenulus/fg2) and in the genus or subgenus *Choroterpides* (belonging to Choroterpes/fg1). Angulate mandibles of Hermanellognatha are just the same as in *Hagenulus* s.str., and simplified maxillae are just the same as in *Choroterpides*. Stricture of labial palp is unique and proves holophyly of Hermanellognatha; in some other taxa with filtering mouth apparatus, setae of maxillary palp are also very long, but they never form such transverse rows as in Hermanellognatha.

(2) Larval pronotum has lateral margins somewhat expanded, each expansion bears a transverse row of stout setae.

(3) Dorsal margin of styliger is produced into a pair of processes dorsad of gonostyli bases.

Classification of Hermanellognatha. Recently it is used to divide Hermanellognatha into genera *Traverella*, *Hylister*, *Hermanella*, *Needhamella*, *Hydrosmilodon*, *Paramaka* and *Leentvaaria*, no one of which has distinct diagnosis based both on larval and imaginal characters. Diagnoses existing in literature (Dominguez et al., 2006, and others) are based on combinations of such characters as shape of larval tergalii, shape of larval maxilla (to separate *Hydrosmilodon*), shape of labial palps (to separate monospecific *Leentvaaria*), shape of imaginal prosternum (to separate monospecific *Needhamella*), shape of male imaginal styliger (to separate monospecific *Paramaka*) and some characters repeating in various genera. Among these characters, shape of styliger and other details in genitals are species-specific and probably do not demonstrate supra-species characters other than the characters of Hermanellonota and Hermanellognatha (see above).



Figs 29–32. Hermanellognatha: 29 — *Hermanella* (*Needhamella*) *saltensis*, subimaginal exuviae of right half of mesonotum; 30–31 — *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**: 30 — fore and hind wings of female imago on the same scale; 31 — hind wing of male imago; 32 — *Hermanella* (*Traverella*) *albertana*, protopenis of mature male larva, ready to moult to subimago, ventral view (left larval cuticular gonoduct and bud of left subimaginal penis lobe are shown by interrupted line).

Рис. 29–32. Hermanellognatha: 29 — *Hermanella* (*Needhamella*) *saltensis*, субимагинальный экзувий правой половины мезонотума; 30–31 — *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**: 30 — переднее и заднее крылья самки имаго в одном масштабе; 31 — заднее крыло самца имаго; 32 — *Hermanella* (*Traverella*) *albertana*, протопенис зрелой личинки самца, готовой к линьке на субимаго, вентрально (левый личиночный кутикулярный гонодукт и зачаток левой доли пениса субимаго показаны прерывистой линией).

Maxilla of *Hydrosmilodon* was characterized by enlarged apical spine and sinuate inner margin; just the same shape of maxilla occurs in "*Traverella* sp.1" sensu Roback [1966] (see *Hermanella chimaera* **sp.n.** below) and some non-related leptophlebiids, particularly *Choroterpes* (*Choroterpides*) sp. from Thailand.

Possibly, natural groups within Hermanellognatha can be characterized by shape of tergalii: *Traverella* has a unique tergalii shape; *Hylister* [including the new species *Hermanella* (*Hylister*) *chimaera* **sp.n.**] has another unique tergalii shape; *Hermanella* s.str. has tergalii shape similar to some others, but also very characteristic; the species formerly placed to the genera *Needhamella*, *Hydrosmilodon* and *Paramaka* have another tergalii shape, which is also not unique, but different from most other leptophlebiids. Only the single species of *Leentvaaria* has tergalii of the most common leptophlebiid type. Basing on this, we can divide Hermanellognatha into subordinate taxa *Traverella*, *Hylister*, *Hermanella* s.str., *Needhamella* s.l. (= *Hydrosmilodon* = *Paramaka*) and *Leentvaaria*. These taxa can have generic ranks (that mostly agrees with the modern tradition), but in this case their doubtful status will lead to continuation of that instability of species binomens, which exists now. I suggest to regard all Hermanellognatha (which includes 25 nominal species only) as a single genus *Hermanella* s.l. and divide it into 5 subgenera — *Hermanella*, *Needhamella*, *Leentvaaria*, *Traverella* and *Hylister*.

1.1.3.1. **Hermanella/fg3**

Hierarchical name: Hermanella/fg3 (sine *Traverella*, *Leentvaaria*, *Needhamella*, *Hylister*; incl. *Guayakia*).

Possible ranking name: subgenus *Hermanella* Needham & Murphy, 1924.

DIAGNOSIS. Each tergalius I–VII has both lamellae 3-pointed, i.e. with terminal process and two side projections; on each lamella (at least of anterior tergalii) terminal process is slender, and two sides projections are wide, pointed and closely adjacent to the terminal process.

SPECIES COMPOSITION. *Hermanella* (*Hermanella*) *froehlichi* Fereira & Dominguez, 1992; *Hermanella* (*Hermanella*) *grandis* Dominguez & Flowers, 1989; *Hermanella* (*Hermanella*) *guttata* Dominguez & Flowers, 1989; *Hermanella* (*Hermanella*) *maculipennis* (Ulmer, 1920 [*Thraulus*]); *Hermanella* (*Hermanella*) *thelma* Needham & Murphy, 1924. The species *costalis* Navas 1934 [*Thraulus*], attributed to *Hermanella* by Peters et al. [2005] is known as imagoes only, and its systematic position is unclear.

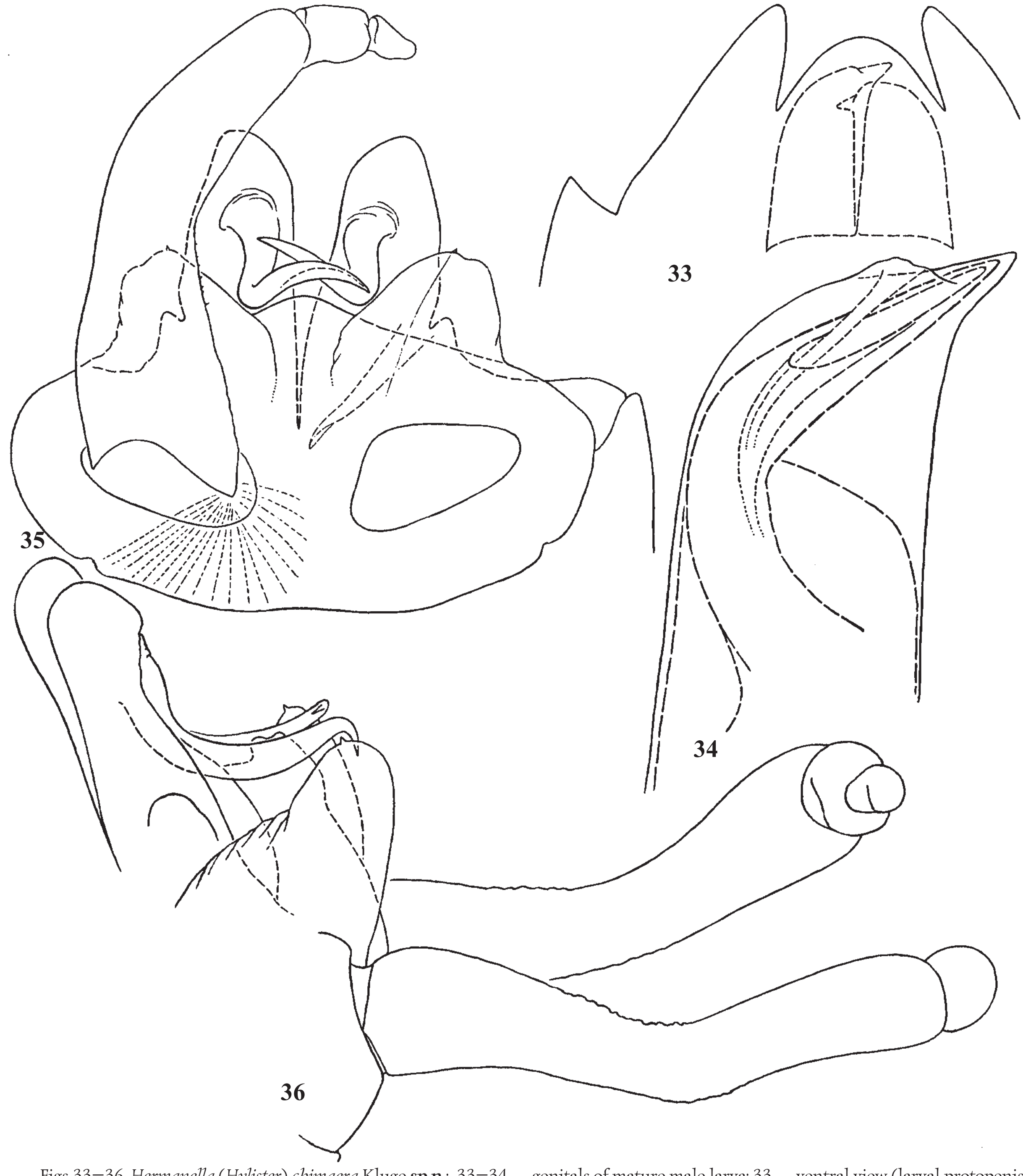
SPECIES EXAMINED. —

1.1.3.2. **Leentvaaria/g(1)**

Hierarchical name: Leentvaaria/g(1).

Possible ranking name: subgenus *Leentvaaria* Demoulin, 1966.

DIAGNOSIS. Tergalii plesiomorphic: each tergalius I–VII has both lamellae simple, narrow, tapering evenly from base to apex and terminating by a single point. Labial palp with enormously elongate 1st and 2nd segments.



Figs 33–36. *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**: 33–34 — genitals of mature male larva: 33 — ventral view (larval protopenis shown by interrupted line); 34 — left lobe of larval protopenis, ventral view (left larval cuticular gonoduct and bud of left subimaginal penis lobe are shown by interrupted line); 35 — genitals of male imago, ventral view (holotype); 36 — the same, lateral view.

Рис. 33–36. *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**: 33–34 — гениталии зрелой личинки самца: 33 — вентрально (личиночный протопенис показан прерывистой линией); 34 — левая доля личиночного протопениса, вентрально (левый личиночный кутикулярный гонодукт и зачаток левой доли пениса субимаго показаны прерывистой линией); 35 — гениталии самца имаго, вентрально (голотип); 36 — то же, латерально.

SPECIES COMPOSITION. *Hermanella* (*Leentvaaria*) *palpalis* (Demoulin, 1966 [*Leentvaaria*]) **comb.n.**

SPECIES EXAMINED. —

1.1.3.3. **Traverella/g1**

Hierarchical name: Traverella/g1 (incl. *Zonda*).

Possible ranking name: subgenus *Traverella* Edmunds, 1948 (= *Zonda* Dominguez, 1995).

DIAGNOSIS. Each tergalius I–VI has both lamellae wide, roundish-triangular, with point apically, bears numerous long slender processes on entire margin; tergalius VII either has similar structure but diminished, or absent.

SPECIES COMPOSITION. *Hermanella* (*Traverella*) *albertana* (McDunnough, 1931 [*Thraulus albertanus*]) (= *Traverella castanea* Kilgore & Allen, 1973); *Hermanella* (*Traver-

ella) *calingastensis* (Dominguez, 1995 [*Traverella* (*Zonda*)]) **comb.n.**; *Hermanella* (*Traverella*) *holzenthali* (Lugo-Ortiz & McCafferty, 1996 [*Traverella*]) **comb.n.**; *Hermanella* (*Traverella*) *lewisi* (Allen, 1973 [*Traverella*]) **comb.n.**; *Hermanella* (*Traverella*) *longifrons* (Lugo-Ortiz & McCafferty, 1996 [*Traverella*]) **comb.n.**; *Hermanella* (*Traverella*) *presidianus* (Traver, 1934 [*Thraulus*]) **comb.n.**; *Hermanella* (*Traverella*) *promifrons* (Lugo-Ortiz & McCafferty, 1996 [*Traverella*]) **comb.n.** Attributed to the genus *Traverella* species *bradleyi* Needham & Murphy, 1924 [*Thraulus*], *montium* Ulmer, 1943 [*Thraulus*], *valdemari* Esben-Petersen ,1912 [*Thraulus*] and *versicolor* Eaton, 1892 [*Thraulus*] are known as imagoes only, so their true systematic position is unclear.

SPECIES EXAMINED**.** *H.* (*T.*) *albertana* (Fig. 32).

1.1.3.4. **Needhamella/g1**

Hierarchical name: Needhamella/g1 (incl. *Hydrosmilodon*, *Paramaka*).

Possible ranking name: subgenus *Needhamella* Dominguez & Flowers, 1989 (= *Hydrosmilodon* Flowers & Dominguez, 1992, = *Paramaka* Savage & Dominguez, 1992).

DIAGNOSIS. Each tergalius has both lamellae oval, often (not always) with a single narrow short terminal process.

SPECIES COMPOSITION. *Hermanella* (*Needhamella*) *antonii* (Sartori, 2005 [*Paramaka*]) **comb.n.**; *Hermanella* (*Needhamella*) *convexus* (Spieth, 1943 [*Thraulus*]) **comb.n.**; *Hermanella* (*Needhamella*) *ehrhardi* (Ulmer, 1920 [*Thraulus*]) **comb.n.**; *Hermanella* (*Needhamella*) *gilliesae* (Thomas & Peru, 2004 [*Hydrosmilodon*]) **comb.n.**; *Hermanella* (*Needhamella*) *mikei* (Thomas & Boutonnet, 2004 [*Hydrosmilodon*]) **comb.n.**; *Hermanella* (*Needhamella*) *primanus* (Eaton, 1892 [*Thraulus*]) **comb.n.**; *Hermanella* (*Needhamella*) *saltensis* (Flowers & Dominguez, 1992 [*Hydrosmilodon*]) **comb.n.**

SPECIES EXAMINED. *H.* (*N.*) *saltensis* (see below).

1.1.3.4.a. ***Hermanella* (*Needhamella*) *saltensis*** (Flowers & Dominguez, 1992) (Fig. 29)

= *Hermanella* (*Hermanellopsis*) sp.: Roback, 1966.

= *Hydrosmilodon saltensis* Flowers & Dominguez, 1992.

MATERIAL EXAMINED: PERU, Prov. HUANUCO: Tingo Maria, Rio Cantaria above Puente Perez, 13–24.I.2006 (N.Kluge): 3 L-S-I♀, 25 L♀ — Prov. JUNIN: near Pichanaki, 6–10.I.2006 (N.Kluge) — 3 L♀.

All collected specimens are females, so it seems that at least in Puente Perez (where 28 specimens were collected), population is parthenogenetic. Roback [1966] reported from the same locality 7 male larvae; possibly, this was a misprint.

Larval and imaginal characters as described by Flowers and Dominguez [1991].

Subimago. Cuticle of mesonotun pigmented, light brown, with sutures lighter (Fig. 29).

1.1.3.5. **Hylister/g(1)**

Hierarchical name: Hylister/g(1).

Possible ranking name: subgenus *Hylister* Dominguez & Flowers, 1989.

DIAGNOSIS. Each tergalius I–VI has both lamellae truncated apically, bearing several long slender processes on apical margin only; tergalius VII either has similar structure but diminished, or absent (Figs 42–44).

SPECIES COMPOSITION. *Hermanella* (*Hylister*) *plaumanni* (Dominguez & Flowers, 1898 [*Hylister*]) **comb.n.** and *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**

SPECIES EXAMINED**.** *H.* (*H.*) *chimaera* (see below).

1.1.3.5.a. ***Hermanella* (*Hylister*) *chimaera*** Kluge **sp.n.** (Figs 30–31, 33–44)

= *Traverella* sp.1: Roback, 1966.

MATERIAL EXAMINED. PERU, Prov. LORETO: Quebrada El Sabalo: right tributary of Rio Itaya at midway between Puente Itaya (57 km by road from Iquitos) and San Joaquin de Omaguas (on Rio Amazon), 1–16.II.2006 (N. Kluge) — 2 L-S-I♂ (among them holotype — 13.II.2006), 2 L-S-I♀, 11 L♀; Rio Itaya above Puente Itaya, 1–16.II.2006 — 1 L-S♂, 2 L♂, 5 L♀, larval exuviae.

Larva. Cuticular pigmentation: light brown, with indistinct, diffuse lighter and darker maculae on head and thorax; femora can be indistinctly darkened at distal part; abdomen has posterior terga darker, anterior terga lighter.

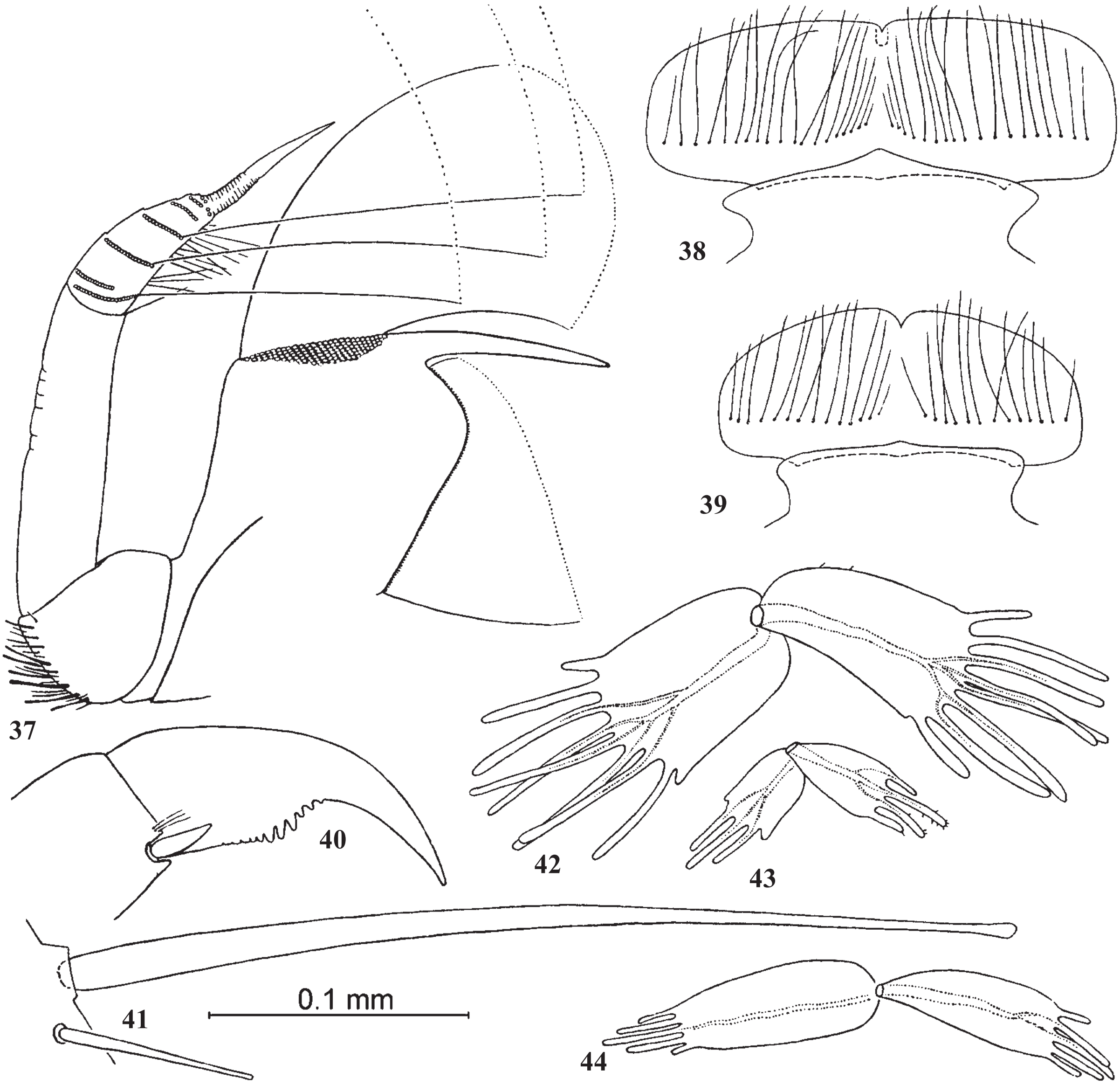
Hypodermal pigmentation: Head and thorax with dark brown maculae; fore and hind protoptera in all instars with reddish-brown bases (as imaginal wings — see below); all femora with dark brown band near apex; first abdominal tergum is dark brown, each tergum II–IX with a narrow brown transverse stripe at posterior margin; each tergum II–VII, besides this, with a pair of brown spots near tergalii bases; caudalii are uniformly coloured, without hypodermal pigment.

Mouth apparatus: Clypeus with a small median protuberance; proportions of labrum are variable (Figs 38–39). Mandibles (angulate — see Hermanellognatha above) have irregularly situated stout setae on proximal 1/2–3/4 of lateral side. Maxilla with apical tusk-like process very long and heavily sclerotized; inner margin of maxilla proximad of tusk is sinuate (Fig. 37).

Trunk: Terga of thorax and abdomen with numerous soft setae; on fore protoptera they form regular rows along veins. Lateral transverse setal row of pronotum (see *Hermanellognatha* above) consists of 5–7 long setae. Posterolateral spines are developed on abdominal segments VIII–IX only. Posterior margins of terga with thin dense spines and the same setae which cover all terga surface. Posterior margin of sternum IX in female convex, without median incision; in male with protogonostyli widely separated (Fig. 33).

Leg setation: Legs with numerous slender clavate setae of variable size (Fig. 41), short bipectinate spine-like setae and long hair-like setae, arranged as following. Fore femur with irregularly situated long and short clavate setae on outer margin and near apex; most surface without setae, inner margin with a few irregularly situated small setae only. Fore tibia on inner side bears dense irregularly situated short spine-like bipectinate setae; one of these setae near apex of tibia is twice longer than others; on dorsal (anterior) side a longitudinal row of clavate setae; on outer side a few small hair-like setae. Fore tarsus with two (preapical and apical) spine-like setae on inner side and a few small hair-like setae on outer side. Middle femur with numerous irregularly situated long and short clavate setae all over dorsal surface, outer and inner margins (the longest on outer margin). Middle tibia with a few spine-like setae on inner side, a longitudinal row of clavate setae on dorsal (anterior) side and dense long hair-like setae on outer side. Middle tarsus with two (preapical and apical) spine-like setae on inner side and hair-like setae on outer side. Hind femur with especially numerous irregularly situated long and short clavate setae all over dorsal surface, outer and inner margins (the longest on outer margin). Hind tibia with an irregular row of spine-like setae on inner side, a longitudinal row of clavate setae on dorsal (anterior) side, a longitudinal row of clavate setae on ventral (posterior) side; outer side with numerous long and short clavate setae and hair-like setae; apex on ventral side with transverse row of non-pectinate stout spine-like setae (pectinate setae on middle and hind tibiae are absent). Hind tarsus with several spine-like setae on inner side and hair-like setae on outer side.

Claws: On each leg claw has one row of small denticles, among which the largest are middle denticles (without enlarged distal denticle) (Fig. 40).



Figs 37–44. *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**, larvae: 37 — maxilla (instead of long setae on palp, apical and median margins, only their bases and tips are shown); 38–39 — clypeus and labrum of different specimens; 40 — claw; 41 — setae on outer margin of femur; 42–43 — right tergalii III and VII; 44 — right tergalius III of specimen from river Itaya; 39–43 — holotype.

Рис. 37–44. *Hermanella* (*Hylister*) *chimaera* Kluge **sp.n.**, личинки: 37 — максилла (вместо длинных щетинок на щупике, апикальном и медиальном краях показаны только их основания и вершины); 38–39 — наличник и верхняя губа разных экземпляров; 40 — коготок; 41 — щетинки на наружном крае бедра; 42–43 — правые тергалии III и VII пар; 44 — правая тергалия III пары экземпляра из реки Итайя; 39–43 — голотип.

Tergalii: All tergalii I–VII are bilamellate, each lamella truncate, with several long processes arising from distal margin only; on each lamella two side processes are often much shorter than others (Figs 42–44); tergalii are progressively diminished from 1st to 6th pair, so that tergalius VI is 1.5 times shorter than the tergalius I; tergalius VII is much smaller, 2 times shorter than tergalius I. In other respects shape of tergalii is variable: in some specimens all tergalii are wide and widened distally, tergalii I–VI bear 5–10 processes on each lamella (Fig. 42), tergalius VII bears 3–5 processes on each lamella (Fig. 43); in specimens from river Itaya all tergalii are narrow, parallel-sided or narrowed distally, with less number of processes — 3–5 on tergalii I–VI (Fig. 44) and 1–3 on tergalius VII. Usually all processes are simple, rarely some processes are bifurcate.

Subimago. Subimaginal cuticle (including mesonotum — see Hermanella/fg1 above) is colourless. Hypodermal coloration as in imago.

Male imago. Upper portion of eye is low, reddish; lower portion is gray. Prosternum with a narrow straight median carina (as in *plaumanni* [*Hylister*] — see Dominguez & Flowers, 1989: Fig. 17). Mesothorax is light brownish. Femora of all legs in most part are white, apical 1/4 is brown or reddish, with a dark brown band separating it from white part. Tibiae and tarsi are white, knee can be reddish; on fore leg apex of tibia and apices of some tarsal segments are brown or

reddish. Fore and hind wings with base diffusely coloured by reddish or brown, the rest part of wing is colourless, veins are pale. Abdominal segment I has tergite dark brown, sternite white; segments II–VI are white, each tergite with a narrow brownish-orange transverse stripe at posterior margin and a pair of small dark brown spots at postero-lateral angles; segments VII–X are bright orange, tergite VII with brown marks as on previous segments. Styliger is orange; gonostyli are white; penis is pale, with sclerotized telopenes darker (see below). Caudalii are white, with brown annulation.

Male genitals. In imago (Figs 35–36): Dorsal margin of styliger forms a pair of large light soft protuberances, each bearing a very small non-sclerotized point on its apex. Penis lobes are deeply divided; laterally, near base, there is a pair of roundish, sclerotized protuberances directed caudally. Telopenes (see diagnosis of Hermanellonota above) are long, strongly bowed medially and bent ventrally, so that gonopores appear to be directed toward penis base. Gonostyli are thick, non-sclerotized, colourless.

In larva: Protogonostyli are widely separated, posterior margin of sternum between them is widely roundish (Fig. 33). Protopenis represents a pair of lobes, whose apices are pointed and stretched apico-medially, so that cross one another; each lobe has a gonopore near its apex laterad of apical point; from gonopore arises a gonoduct lined by larval cuticle. Subimaginal penis develops inside larval protopenis as shown in Fig. 34.

Female imago. Unlike male, legs are not white, but dull-orange; all femora with brow subapical bands as in male. Abdominal tergite I is dark brown, other terga and sterna are entirely orange; terga II–VII with brown marks as in male.

Dimensions. Lenght of fore wing (and approximated length of body) 5–7 mm.

COMPARISON. Shape of maxilla of the new species (very long maxillary tusk and sinuate inner margin) is the same as in the species which were attributed to the genus *Hydrosmilodon* Flowers & Dominguez, 1992 — *primanus* Eaton 1892 [*Thraulus*], *saltensis* Flowers & Dominguez, 1992 [*Hydrosmilodon*], *gilliesae* Thomas & Peru, 2004 [*Hydrosmilodon*], and *mikei* Thomas & Boutonnet, 2004 [*Hydrosmilodon*]. Just the same shape of maxilla occurs in non-related taxa (particularly, in some *Choroterpides*), so this character is poorly species-specific, and can not be used to characterize supra-species taxa. Shape of tergalii of the new species is the same as in *plaumanni* Dominguez & Flowers, 1989 [*Hylister*], which was placed into a monospecific genus *Hylister* Dominguez & Flowers 1989. Such shape of tergalii is not found in any other mayflies, and testifies about close relationship of these two species. Besides shape of maxilla, larva of the new species differs from *plaumanni* [*Hylister*] by presence of median process on clypeus and absence of enlarged distal denticle on larval claw. Male imago of the new species differs from *plaumanni* [*Hylister*] and all other Hermanellini by more complicatedly curved telopenes.

The new species has marked variability: larvae collected in Itaya (a medium-size river with strong current) are small (5 mm), with narrow tergalii (Fig. 44); larvae collected in El Sabalo (a small stream, mostly hidden in forest) are larger (7 mm), with wide tergalii (Fig. 42). However, male adults reared from larvae of the both forms are similar, particularly have the same unusually bent telopenes (Figs 35–36), that allows to regard them to be conspecific.

ACKNOWLEDGEMENTS. The work was supported by federal program "Leading Scientific Schools", project No. НШ 7130.2006-4.

References

Demoulin G. 1966. Contribution à l'etude des Ephéméroptères du Surinam // Bull. Inst. Roy. Sci. Nat. Belg. T.42. N.37. P.1–22.

Domínguez E. 1999. Systematics, cladistics and biogeography of the American genus *Farrodes* (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) // Zoological Journal of the Linnean Society. Vol.126. P.155–189.

Domínguez E. & Flowers R.W. 1989. A revision of *Hermanella* and related genera (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) from Subtropical South America // Annals of the Entomological Society of America. Vol.82. P.555–573.

Domínguez E., Molineri C. & Peters W.L. 1996. Ephemeroptera from Central and South America: New species of the *Farrodes bimaculatus* group with a key for the males // Studies on Neotropical Fauna and Environment. Vol.31. P.87–101.

Domínguez E., Peters W.L., Peters J.G. & Savage H.M. 1997. The imago of *Simothraulopsis* Demoulin with a redescription of the nymph (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) // Aquatic Insects. Vol.19. P.141–150.

Domínguez E., Molineri C., Pescador C., Hubbard M. & Nieto C. 2006. Ephemeroptera of South America // Aquatic Biodiversity in Latin America. Vol. 2 // Pensoft: Sofia-Moscow. 646 pp.

Kluge N.J. 1994a. A revision of Leptophlebiidae of Cuba (Insecta, Ephemeroptera) // Zoosystematica Rossica. Vol.2. No.2. P.247–285.

Kluge N.J. 1994b. Habrophlebiinae subfam. n. with description of a new species of *Habroleptoides* from Caucasus (Ephemeroptera: Leptophlebiidae) // Zoosystematica Rossica. Vol.3. No.1. P.35–43.

Kluge N.J. 1999. A system of alternative nomenclatures of the supraspecific taxa. Linnaean and post-Linnaean principles of systematics // Entomol. Obozrenie (Rev. Entomol. URSS). Vol.78. No.1. P.224–243 (in Russian); English translation in: Entomol. Review. Vol.79. No.2. P.106–110.

Kluge N.J. 2000. Modern systematics of insects. Part I. Principles of systematics of living organisms and general system of insects with classification of primary wingless and paleopterous insects // Lan': S-Petersburg. 336 pp. (in Russian)

Kluge N.J. 2004. The phylogenetic system of Ephemeroptera // Kluwer Academic Publishers. 456 pp.

Peters W.L. 1971. A revision of the Leptophlebiidae of the West Indies (Ephemeroptera) // Smithsonian Contributions to Zoology. Vol.62. P.1–48.

Peters W.L. 1980. Phylogeny of the Leptophlebiidae (Ephemeroptera): an introduction // In: J.F. Flannagan & K.E. Marshall (eds.). Advances in Ephemeroptera Biology (Proc. 3rd Int. Conf. Ephemeroptera, 4–10 July 1979, Winnipeg, Canada). Plenum Press: New York. P.33–41.

Peters J.G., Flowers R.W., Hubbard M.D., Domínguez E & Savage H.M. 2005. New records and combinations for Neotropical Leptophlebiidae (Ephemeroptera) // Zootaxa. No.1054. P.51–60.

Peters W.L., Gillies M.T. 1995. Square facets in a hexagonal world. Current directions in research on Ephemeroptera // In: L.D. Corkum & J.H. Ciborowski (eds.). Current directions in research on Ephemeroptera (Proc. 7th Int. Conf. Ephemeroptera, 3–6 August 1992, Orono, Maine, USA). Canadian Scholar's Press Inc.: Toronto. P.371–375.

Roback S.S. 1966. The Catherwood Foundation Peruvia-Ama-zon expedition. VI — Ephemeroptera nymphs // Monogr. Acad. Nat. Sci. Philad. Vol.14. P.129–199.

Savage H.M. 1986. Systematics of the *Terpides* lineage from the Neotropics: Definition of the *Terpides* lineage, methods, and revision of *Fittkaulus* Savage & Peters // Spixiana. Vol.9. P.255–270.

Savage H.M. 1987. Biogeograhic classification of the neotropical Leptophlebiidae (Ephemeroptera) based upon geological centres of ancestral origin and ecology // Stud. Neotrop. Fauna and Environment. Vol.22. No.4. P.199–222.

Savage H.M. & Peters W.L. 1983. Systematics of *Miroculis* and related genera from northern South America (Ephemeroptera: Leptophlebiidae) // Transactions of the American Entomological Society. Vol.108. P.491–600.

Traver J.R. 1947. Notes on Neotropical mayflies. Part II. Family Baetidae, subfamily Leptophlebiinae // Revista de Entomologia. Vol.18. P.149–160.

Traver J.R. 1959. Uruguayan mayflies. Family Leptophlebiidae: Part I // Revista de la Sociedad Uruguaya de Entomologia. Vol.3. P.1–13. Pl.1–3.